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Behavioural interactions between predators and their prey in marine ecosystems

Interactions comportementales entre les prédateurs et leurs proies dans les écosystèmes marins

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ABSTRACT

The presence of a predator may impact the abundance of their prey through non-lethal means by inducing changes in the phenotype or traits of the prey. Such interactions arise because individuals are faced with a common trade-off, between predation risk and some aspect of their life history strategy, e.g. energy intake or reproduction. Non-lethal interactions in terrestrial and freshwater ecosystems are common and their importance has been demonstrated, but there is a lack of studies for marine ecosystems particularly among top predators. To assess our current knowledge of non-lethal interactions between top marine predators and their prey a survey of the ecological literature was conducted. Twelve studies were found that detailed changes in habitat use and activity levels according to predation risk. Most studies involved the disruption of foraging behaviour but three studies reported the disruption of reproductive behaviour. The lack of studies on non-lethal interactions between large marine predators and their prey is likely not a reflection of their ecological importance, but rather a reflection of the difficulty of studying such interactions in large species in an ocean environment. A better understanding of the prevalence and magnitude of non-lethal interactions in marine communities is needed to better understand the full impact of predators on prey populations.

RÉSUMÉ

La présence d'un prédateur peut avoir une incidence sur l'abondance de ses proies par le biais de mécanismes non létaux en induisant des changements dans le phénotype des proies ou leurs caractères. De telles interactions comportementales surviennent parce que les individus doivent consentir à un compromis entre le risque de prédation auquel ils sont confrontés et un certain aspect de leur cycle biologique (p. ex, l'apport énergétique ou la reproduction). Les interactions non létales dans les écosystèmes terrestres et d'eau douce sont courantes et leur importance a été démontrée, mais on manque d'études à ce chapitre pour les écosystèmes marins, en particulier chez les prédateurs de niveau trophique supérieur. Pour évaluer nos connaissances actuelles des interactions non létales entre les prédateurs marins de niveau trophique supérieur et leurs proies, nous avons dépouillé la documentation en matière d'écologie pour trouver douze études décrivant les changements dans les niveaux d'activité et l'utilisation de l'habitat selon le risque de prédation. Bien que la plupart des études traitent de la perturbation du comportement alimentaire, trois d'entre elles concernent la perturbation du comportement reproducteur. Le manque d'études sur les interactions non létales entre les grands prédateurs marins et leurs proies n'a sans doute aucun lien avec leur importance écologique. Il serait plutôt lié à la difficulté d'étudier de telles interactions chez les grandes espèces dans un environnement océanique. Une meilleure compréhension de la prévalence et de l'ampleur des interactions non létales dans les communautés marines est essentielle si nous voulons parvenir à mieux comprendre pleinement l'effet des prédateurs sur leurs proies.

Introduction

The dynamic interactions between predators and prey are an integral theme in population ecology. Traditionally, predator-prey interactions have been viewed as lethal whereby a predator consumes prey and directly changes prey abundance (i.e., density-mediated interactions; Abrams et al., 1996). Density-mediated interactions have greatly contributed toward our understanding of community dynamics and species diversity (e.g., Paine, 1966). However, the mere presence of a predator may also impact the abundance of their prey by inducing changes in the phenotype of prey, such as their behaviour (i.e., trait-mediated interactions, Abrams et al., 1996). Trait-mediated interactions arise because individuals are faced with a trade-off: one of minimizing predation risk while maximizing some aspect of their life history strategy, e.g. energy intake or reproduction (Lima and Dill, 1990; Werner and Peacor, 2003).

Behavioural decisions by individuals that involve maximizing energy intake often increase the risk of predation through increasing activity levels and thereby increasing the probability of an encounter with a predator or detection by a predator (Lima and Dill, 1990). The benefit of an increase in anti-predator behaviours, such as the use of a refuge, lower activity levels, or increased vigilance (Lima and Dill, 1990), is a reduction in predation risk. For example, Skelly (1994) showed that the low activity level of wood frog (*Rana sylvatica*) larvae lowers the predation risk from dragonfly (*Anax junius*) larvae. The costs associated with anti-predator behaviours are a reduction in energy intake, either due to a decrease in foraging activity or moving to a less favourable foraging habitat, which ultimately may increase mortality (Lima, 1998). Werner et al. (1983) have demonstrated that in the presence of largemouth bass (*Micropterus salmoides*) predators, small bluegill sunfish (*Lepomis macrochirus*) choose less favourable foraging habitat to avoid predation leading to a significant reduction in growth and a potentially increased mortality rate.

Given that foraging decisions must meet the conflicting demands of prey acquisition and predator avoidance, and that predator avoidance is energetically costly, we can expect the level of risk taking to be state-dependent, i.e. dependent on the body size or condition of the individual. Metcalfe et al. (1998) found that Atlantic salmon (*Salmo salar*) showed a preference to feeding at night to reduce predation risks despite suffering from a lower foraging efficiency. However, the extent of this preference was influenced by the physiological state of the individual and the life history stage. Individuals that were preparing to migrate, particularly those of a small body size, spent a greater proportion of their time foraging during the day. Of the individuals that had delayed migration, only those in a poor physiological condition spent the greater proportion of their time foraging during the day.

The trade-off between predation risk and energy intake is further complicated by changes in the hunting strategy of predators creating temporal variation in predation risk (Lima, 2002). Predators may change their strategy according to whether they hunt in response to prey density, to the resource of the prey, or according to environmental conditions. A good example comes from the terrestrial literature. Post and Peterson (1999) have shown that on Isle Royale, Michigan, during heavy snow years, wolves (*Canis lupus*) cause large reductions in the moose (*Alces alces*) population due to hunting in large packs along lakeshores where moose aggregate due to their restricted movements in heavy snow. During years of low snowfall the impact of wolves is less

severe since moose are more scattered, wolves hunt in smaller packs to increase their efficiency at finding their prey but moose, due to the lower snowfall, are better at avoiding or escaping from encounters with wolves. Thus, the optimal trade-off between predation risk and energy intake is likely to vary greatly among individuals and involve a complex interplay of both predator and prey traits that may vary temporally.

Although there have been numerous studies examining the trade-off between predation risk and energy intake, far fewer have examined the implications for reproductive behaviour and success (*see reviews*: Lima and Dill, 1990; Magnhagen, 1991; Sih, 1994). Similar to the case with energy intake, traits and activities that increase reproductive success, e.g. large body size, sexual ornamentation, and searching for mates, increase the risk of predation (Sih, 1994). The trade-off between reducing predation risk and maximizing reproductive success has led to adaptive changes in prey traits (Magnhagen, 1991; Sih, 1994).

Female mating strategies typically involve a large element of mate choice whereas male mating strategies typically involve elements of courtship or dominance displays, mate search and defense. If females and males increase their risk of predation through their mating behaviour and displays, mate choice might be affected leading to lowered fecundity and diminished sexual selection (Sih, 1994). Forsgren (1992) demonstrated that female sand gobies (*Pomatoschistus minutus*), in the presence of the predator cod (*Gadus morhua*), showed a preference toward smaller and duller males compared to the situation when no predators were present. Further, Forsgren and Magnhagen (1993) showed that in the presence of cod, male sand gobies reduced the amount of time spent in courtship thus increasing the chances of females mating with lower quality males and reducing their fecundity. Berglund (1993) showed that in pipefish (*Syngnathus typhle*) where males are the limiting sex, males were less choosy of females in the presence of a predator. Sih (1994) discusses the risks associated with primary mating tactics, such as female defense, and suggests that less risky alternative mating tactics, such as sneak copulations, may increase in frequency when predation risks are high. Thus, reproductively active individuals are likely to change those reproductive traits that increase the risk of predation.

The predator-prey interactions discussed above are direct interactions and defined according to Abrams (1995) as "A species (the "initiator" of the effect) has a direct effect on another (the "receiver" of the effect) if a change in some property of the initiator species produces a change in a property of the receiver, and this change does not require a change in any property of any other species to occur". Given that the dynamics of prey are linked to the dynamics of other species (i.e., the preys' resources and competitors) lethal or non-lethal impacts on prey traits may indirectly affect the abundance of other species. Predator-prey effects are indirect "...if a change in some property of another (or several other) species (the "transmitter[s]") are caused by the change in the initiator's property (properties) and are required to produce the change in the property of the receiver species" (Abrams, 1995). Turner and Mittelbach (1990) investigated trait-mediated indirect interactions between largemouth bass predators, small bluegill sunfish, and zooplankton. In the presence of bass, the abundance of three cladoceran species (*Daphnia*, *Diaphanosoma* and *Ceriodaphnia*) and the phantom midge *Chaoborus* increased relative to their abundance when bass were absent. This was not due to an increase in predation by bass on bluegills but rather to a decrease in bluegill foraging activity to reduce the predation risk from bass. Rahel and Stein (1988)

examined trait-mediated indirect interactions between the prey fish johnny darter (*Etheostoma nigrum*) and two of its predators, crayfish (*Orconectes rusticus*) and smallmouth bass (*M. dolomieui*). In the presence of bass, darters decreased their activity levels and spent more time hiding in shelters to reduce predation risk. In the presence of crayfish, the activity of darters was similar to that of a control. However, when both predators were present, crayfish indirectly increased predation by bass on darters by increasing the activity levels of darters through approaching and forcing them to move, and evicting darters from shelters. Bass indirectly increased predation by crayfish by causing darters to seek shelter and increasing their exposure to crayfish. Thus, to fully understand and assess the impact of a predator on its prey, one must account for both direct and indirect non-lethal effects (Wootton, 1994; Lima, 1998; Werner and Peacor, 2003).

Trait-mediated interactions are common in terrestrial and aquatic communities (Lima and Dill, 1990; Lima, 1998; Werner and Peacor, 2003), but far fewer studies have reported such interactions in marine communities, particularly for top marine predators such as sharks, pinnipeds and large predatory fish (Lima and Dill, 1990; Dill et al., 2003). Given the collapse of several pelagic fisheries (Myers and Worm, 2003) and the dramatic decline in some top marine predator species, e.g. sharks (Baum et al., 2005), assessing the relative importance of these predator-prey interactions in marine communities is clearly a critical requirement for effective management and conservation strategies (Dill et al., 2003). To assess our current knowledge of trait-mediated interactions in sharks, pinnipeds and large predatory fish, a survey of the ecological literature was conducted.

Methods

To locate relevant studies we searched the online databases Biological Abstracts and Aquatic Sciences and Fisheries Abstracts for the following keywords: behavioural cascades, behavioural shifts, density-mediated interactions, gadoid, interference, marine, mating behaviour, pinniped, predation, predation risk, predator, prey interactions, reproductive behaviour, seal, shark, trait-mediated interactions and trophic cascades. Papers whose title and abstract were relevant were read and cited literature scanned for relevant references. We also conducted the same searches in the following journals: American Naturalist, Ecology, Marine Mammal Science, Oecologia, Oikos and Trends in Ecology and Evolution.

Results

We found few studies on trait-mediated interactions on sharks, pinnipeds, and large predatory fish (Table 1). Three studies involved trait-mediated interactions between pelagic fish species, three between cetaceans and their prey, and five on trait-mediated interactions between tiger sharks (*Galeocerdo cuvier*) and the Indian Ocean bottlenose dolphin (*Tursiops aduncus*), green turtle (*Chelonia mydas*) and the dugong (*Dugong dugon*). Finally, one study modelled trait-mediated interactions in the North Pacific harbour seal (*Phoca vitulina*) with a view to understanding the population decline of this species in the Gulf of Alaska. These twelve studies detailed changes in habitat use and activity levels. Most studies described the disruption of foraging behaviour, but three studies reported the disruption of reproductive behaviour (Table 1).

Foraging behaviour and anti-predator behaviour

Pitcher et al. (1996) and Nottestad et al. (2002) demonstrated that the anti-predator behaviour of herring (*Clupea harengus*) in coastal and offshore areas of the Norwegian Sea differed according to the type of predator. In the coastal areas, herring are exposed to predation by individual cod (*Gadus morhua*), small groups of haddock (*Melanogrammus aeglefinus*) and dense fast moving schools of saithe (*Pollachius virens*). Pitcher et al. (1996) found that when the herring were attacked by individual cod or haddock, they modified their school structure to allow individuals to continue foraging while keeping the risk of predation low through schooling. However, when attacked by saithe, which break up the school and consume more herring than individual cod or haddock, the herring dove 150m or more to avoid further attack. Consequently, the herring incurred energy losses through cessation of foraging, diving and returning to the surface and increased predation risk while the school was re-formed. In offshore areas, herring are exposed to predation by marine mammals, namely fin whales (*Balaenoptera physalus*), Atlantic white-sided dolphins (*Lagenorhynchus acutus*) and killer whales (*Orcinus orca*). Nottestad et al. (2002) found that during the day the herring formed dense aggregations in deep waters to reduce encounters with marine mammals, while during the night the herring foraged closer to the surface. Lima and Bednekoff (1999) suggest that prey that are exposed to brief periods of high predation risk should exhibit their strongest anti-predator behaviours only when the risk of predation is high and aggregate to forage when the risk is low. With reference to Lima and Bednekoff (1999), Nottestad et al. (2002) suggest that the differences in anti-predator behaviour between coastal and off-shore herring are due to the brief and infrequent high-risk predatory events from marine mammals compared with the more frequent but lower mortality events from cod, haddock and saithe. Thus, herring appear to be able to assess the risks of predation from different predators and adjust their behaviours accordingly to minimise that risk.

Frid et al. (2006) used a dynamic, state-variable model to explore the relationship between resource availability and predation risk in North Pacific harbour seals. The study was designed to explore the reasoning behind the dramatic population decline in the harbour seal population in Prince William Sound, Alaska between 1984 and 1997 and for its continued failure to recover. The results from the model showed that a decrease in resource availability (herring, *C. pallasi*, and walleye pollock, *Theragra chalcogramma*) led to an increase in trait-mediated effects; seals spent less time hauled out and more time in foraging areas, had longer dives and consequently longer surface intervals between dives to replenish oxygen stores. These changes led to an increase in density-mediated effects due to greater predation by killer whales and Pacific sleeper sharks (*Somniosus pacificus*) despite constant predator density. Further, these effects were amplified in individuals that were of a lower body condition since they were more likely to increase their foraging effort despite increased predation risks to recover energy reserves. These results help explain why resource-sensitive states of individuals, such as maternal postpartum mass, in a depleted population remain constant (e.g., Sable Island harbour seals, Bowen et al., 2003). Over-exploitation of fish stocks is predicted to increase predation rates on harbour seals since individuals, particularly those in poor condition, will be forced to increase their foraging effort and thus increase their risks of predation. Frid et al. (2006) suggest that understanding the effect of commercial

fisheries on seal populations, and the latter's effect on fish stocks, might be improved if fishery population models took into account estimates of the distribution of the energy state of seals in the population and the indirect effects of their predators.

Habitat use, foraging behaviour and anti-predator behaviour

Gotceitas et al. (1995) found that juvenile cod in the presence of older cod predators, showed a strong preference for cobble or kelp habitat whereas when older cod were present but were passive, the juvenile cod preferred a finer grained mineral substrate. Given that juvenile cod are active predators, hiding in cobble may lower their foraging efficiency. These results suggest that juvenile cod are able to assess the risk from predation when in the presence of a potential predator.

Recently, a series of studies have examined the use of habitat by tiger sharks and their prey, the Indian Ocean bottlenose dolphin, green turtle and the dugong in Shark Bay, Western Australia. Heithaus and Dill (2002) and Heithaus and Dill (2006) found that during the cold months when tiger sharks were mostly absent from Shark Bay, bottlenose dolphins showed a strong preference to shallow habitats reflecting the distribution and abundance of their prey (teleost fish). During the warm months when the risk of shark predation was high, dolphins preferred deeper habitats despite lower prey availability. Further, when foraging in shallow habitats in the presence of sharks, dolphins preferred edge microhabitats rather than the interior despite a lower presence of sharks in the latter. They suggest that dolphins are able to assess the intrinsic risk of predation in a microhabitat such that they show preference to edge habitats because of the greater potential for escape compared with interior microhabitats. Heithaus and Dill (2002) suggested the existence of a trait-mediated indirect interaction between bottlenose dolphins, tiger sharks and the shark's main prey, sea turtles, dugongs and sea snakes. Although dolphins are frequently attacked by sharks they comprise only a small part of the diet. The distribution and abundance of tiger sharks is largely driven by sea temperature and the distribution of prey. Thus, although the shark's main prey do not directly interact with dolphins, they do so indirectly by influencing the distribution of tiger sharks and therefore dolphin distribution. Finally, the study also found that tiger sharks influenced the size of dolphin groups. In shallow habitats, dolphin group size was larger than in deeper habitats and foraging dolphins occurred in smaller groups compared with resting dolphins (a behaviour that poses a high risk of predation).

Heithaus et al. (2007) showed that habitat use by green turtles was also influenced by predation risk, but the risk taken was dependent on body condition. Turtles in poor condition used forage-rich microhabitats even though they were exposed to higher predation risks by tiger sharks, while individuals in good body condition used shallow forage-poor microhabitats with a lower risk of predation. Wirsing et al. (2007b) demonstrated that habitat preferences in the dugong were largely governed by ease of escape. Dugongs showed a preference to edge microhabitats even though this was the preferred habitat for tiger sharks and offered low food availability. However, edge habitats had numerous escape routes whereas interior microhabitats, which are forage-rich and have low predation risks, offer few escape routes. The foraging behaviour of dugongs is also influenced by the risk of predation (Wirsing et al. 2007a). Dugongs exhibit two tactics while foraging on sea grass species in shallow habitats. Cropping involves removing clusters of leaves from the branches of sea grass and is used while foraging on temperate species (primarily *Amphibolis antarctica*) that are very abundant.

Excavation involves digging the plant out and consuming both above- and under-ground parts and is used on the less common but more energy- and nutrient-rich tropical species. During cropping, dugongs are able to scan for predators but excavation requires extended periods of time when the dugong is unable to be vigilant and creates sediment plumes that obscures their vision and may indeed attract predators. The study found that when large tiger sharks were present in the area, dugongs significantly reduced the amount of time spent excavating The fore-mentioned studies also suggested the occurrence of trait-mediated indirect interactions between tiger sharks, their prey (sea turtles and dugongs) and the resources consumed by their prey, sea grass. Through grazing, sea turtles and dugongs can dramatically alter the species composition of sea grass communities (particularly when dugongs excavate plants) and, in turn, the composition of invertebrates that reside in those communities. Thus, microhabitats that suffer from high sea turtle and dugong grazing pressure due to low tiger shark abundance will have different species assemblages to those areas that suffer from lower grazing pressure and higher tiger shark abundance.

Changes in reproductive behaviour

Smale et al. (2001) examined the behavioural interactions between a suite of predators and inshore mating and spawning chokka squid (*Loligo vulgaris reynaudii*). Of the predators (cephalopods, teleost fish, chondrichthyians and marine mammals), marine mammals incited the most acute disruption of egg laying while the other predators caused more chronic disruption due to spending more time on the spawning grounds. When seals or dolphins were present at the spawning grounds, the squid moved away from the spawning area and did not return until minutes, and on one occasion at least one hour, after the predators had left.

Predators may also influence the reproductive behaviour of their prey through sound. When foraging in sea grass beds or over sand, bottlenose dolphins (*T. truncatus*) emit low frequency 'pops' and respond to sounds emitted by their prey. Male Gulf toadfish (*Opsanus beta*), an important dietary component of bottlenose dolphins, breed in sea grass habitats and call to attract mates. Remage-Healey et al. (2006) have shown that when toadfish are within the hearing range of the low frequency 'pops' emitted by foraging dolphins, the rate of courtship calling is significantly reduced. Similar results were found in mating male silver perch (*Bairdiella chrysoura*) in the presence of bottlenose dolphins (Luczkovich et al., 2000).

Discussion

Many studies on trait-mediated interactions were found for terrestrial, freshwater and marine inter-tidal zone communities (Lima and Dill, 1990; Magnhagen, 1991; Sih, 1994; Abrams, 1995; Abrams et al., 1996; Kats and Dill, 1998; Lima, 1998; Dill et al., 2003; Werner and Peacor, 2003) and provided clear evidence of their importance in community dynamics. Despite their potential importance, a dearth of studies was found on such interactions between sharks, pinnipeds and large predatory fish and their prey. The primary reason for this scarcity is that to document and measure the extent of trait-mediated interactions, the lethal effect must be removed while keeping the predator in the system to measure the direct and indirect effects due to predator-induced changes in the preys' traits. In terrestrial and particularly in freshwater and inter-tidal zone communities this is achievable (e.g., Killen and Brown, 2006) but it is far more difficult in

an ocean environment with predators that are large, often inaccessible and typically move over large areas (Lima 1998).

A common way to assess the impact of trait-mediated interactions is to expose the prey to the predator but prevent the predator from consuming the prey either by manipulation of the predators' mouthparts (e.g., Schmitz et al., 1997) or placing the predator in a cage (e.g., Peacor and Werner, 2001). Schmitz et al. (1997) assessed the total predator effect of spiders and the relative effects of density and trait-mediated interactions on their prey, grasshoppers, and the prey's resource, herbaceous plants. Through gluing the spider's chelicerae to prevent consumption, Schmitz et al. (1997) were able to show that the indirect effects arising from anti-predator behaviour by grasshoppers produced the same magnitude of grasshopper mortality, due to lower energy intake, and impact on herbaceous plants as those generated by lethal effects. An alternative method to measuring trait-mediated interactions is to add and then remove predators from the interaction to enable one to measure both the direct and indirect effects. For example, the study of Rahel and Stein (1988), previously discussed, was able to measure the indirect interaction effects of both bass and crayfish on darters, and the individual direct effects of each predator by removing one from the interaction. These two approaches to measuring density- or trait-mediated interactions are clearly not possible with large marine predators, either in an ocean or laboratory environment. To complicate matters further, there are numerous variables that can influence the magnitude of density- and trait-mediated interactions (Peacor and Werner, 2001; Luttbeg et al., 2003; Peacor and Werner 2003). For example, the density of the prey and of the resources they feed upon can influence the magnitude of the non-lethal predator effect on the prey (Peacor and Werner 2003). Thus, environmental variability in the availability of resources can determine the magnitude of density- and trait-mediated interactions between predator and prey. Designing experiments that investigate interactions between a single prey and predator species will ignore the potential effects of other prey and predator species on the interaction. For example, intimidation by crayfish causes johnny darters to forage in open water thus facilitating predation by bass (Rahel and Stein, 1988), an indirect interaction that would not be observed in a single predator-prey experiment. Other variables such as the state and life history stage of the predator and prey and the duration of the study will impact the magnitude of these interactions (Luttbeg et al. 2003). Nevertheless, studies created on a small spatial and temporal scale can contribute toward our understanding of larger scale processes (Lima 1998).

Recently, several studies on sharks and their prey (marine mammals and turtles) have used the theory of the Ideal Free Distribution (IFD) to measure the influence of predation risk on the foraging behaviour of the predator's prey (reviewed in Wirsing et al., 2008). Under the IFD, individuals should distribute themselves among patches of food according to the availability of that food such that all individuals experience the same rate of food intake. Once the availability of food and the level of predation risk in given patches have been measured, differences in the use of patches by individuals can be explained in terms of the predation risk associated with a given patch. Combining measures of prey availability and predation risk among patches with the use of telemetry instruments, e.g. satellite-linked transmitters to measure the amount of time devoted by a given individual to a given patch, one should be able to examine the trade offs between foraging and predation risk for marine mammals and large fish.

The potential importance of trait-mediated interactions among sharks, seals and large predatory fish and their prey is clear when one examines the strength of trait-mediated effects relative to lethal effects in other predator-prey communities, how the magnitude of these effects in aquatic ecosystems compares with those in terrestrial ecosystems and the outcome of these effects for the local and whole population. Several studies have shown that trait-mediated effects are as strong as or stronger than lethal effects, even when the lethal effects are high (*see reviews*: Peacor and Werner, 2001; Werner and Peacor, 2003; Preisser et al., 2005). The reasons for this are because trait-mediated effects act on prey independent of the lethal effects, i.e. they arise through prey that remain in the community while lethal effects arise through removing prey from the community. Thus, a lower foraging effort by prey due to the presence of a predator leads to a lower energy intake and a reduction in the impact of the prey on its resource, irrespective of the level of predation. Secondly, the effects of trait-mediated interactions are immediate, act on all prey in the community and for their lifetime, even on those that are ultimately removed through predation, and may target other species in the community through behavioural cascades (Peacor and Werner, 2001; Dill et al., 2003; Peacor and Werner, 2003).

Preisser et al. (2005) have shown that trait-mediated interactions are strongest in marine communities and weakest in terrestrial communities in two-level food chains. This pattern is even stronger in three-level food chains. Several reasons have been proposed to explain these observations including the possibility that marine organisms are more capable of assessing the risks from predation due to more easily perceived visual or chemical characteristics of their predators, or that aquatic organisms invest in more costly predator defense strategies.

Changes in habitat use in response to predation risks can lead to changes in both local and whole population distribution (Lima 1998). Studies on stream and lake communities have contributed greatly to our understanding of the effects of trait-mediated interactions on populations, and have shown that prey distribute themselves according to the habitat preferences of their predators (Lima 1998). For example, in stream systems fewer prey are found in deep pools that are favoured by predators while more are found in the shallow riffles that connect pools. Prey distribution may also be influenced by the agility of the predator; risks associated with emigration in response to predation may be greater in the presence of agile vertebrate predators than less agile invertebrate predators. Indeed, it has been suggested that predators in predator-prey interactions should be categorized according to their level of agility (pelagic, i.e. more mobile vs. benthic, i.e. less mobile) rather than based on their taxonomy, e.g. vertebrate vs. invertebrate (Lima 1998). The presence of vegetation cover and other types of refuge for hiding from predators will also likely influence prey distribution. It is quite clear that the lack of studies on trait-mediated interactions between large marine predators and their prey is not a reflection of their ecological importance but rather a reflection of the difficulty of studying such interactions in large species in an ocean environment. A better understanding of the prevalence and magnitude of trait-mediated interactions is needed in marine communities to better understanding the full impact of predators on their prey and to design management and conservation strategies.

Table 1 Summary of studies designed to measure trait-mediated interactions (TMIs) between cetaceans, sharks, pinnipeds and large predatory fish and their prey.

Reference	Predator	Prey	Resource	TMI Description	Food-chain	Mechanism of TMI
Gotceitas et al., 1995	Cod (+3 years)	Cod (+0 years)		Juvenile cod change habitat preference in presence of older cod	2	Change of habitat
Pitcher et al., 1996	Cod, haddock, saithe	Herring		Herring school in the presence of cod and haddock, and dive deep in the presence of saithe	2	Change of habitat
Luczkovich et al., 2000	Bottlenose dolphin	Silver perch		Loudness of mating calls diminished in presence of dolphins	2	Change of behaviour
Smale et al., 2001	Cephalopods, teleosts, chondrichthyians, marine mammals	Squid		Disruption of mating and egg-laying through leaving spawning grounds	2	Change of habitat
Heithaus and Dill, 2002	Tiger shark	Bottlenose dolphin	Teleost fish	Dolphins avoid habitats with high predation risk and occur in larger groups when exposed to high risk.	3	Change of habitat. Increase group size
Nottestad et al., 2002	Fin whale	Herring		Herring swim in large, dense shoals deep in the water column	2	Change of habitat
Frid et al., 2006	Killer whale, Pacific sleeper shark	Pacific harbour seal		With a decrease in resource levels, harbour seals increase time spent foraging and time spent in dives and at the surface between dives, thus increasing the predation risk	2	Change in activity levels
Heithaus and Dill, 2006	Tiger shark	Bottlenose dolphin	Teleost fish	Decreased use of dangerous but productive habitats when sharks present. Dolphins showed preference to shallow edge habitats due to lower intrinsic risk	3	Change of habitat
Remage-Healey et al., 2006	Bottlenose dolphin	Gulf toadfish		During mating, toadfish decrease their rate of courtship calling to minimise predation risk	2	Change of behaviour
Heithaus et al., 2007	Tiger shark	Green sea turtles	Sea grass	Turtles in poor body condition select forage-rich habitats with high predation risk. Turtles in good body condition select forage-poor habitats with low predation risk.	3	State-dependent selection of habitat
Wirsing et al., 2007b	Tiger shark	Dugong	Sea grass	Dugongs use forage-poor edge habitats when tiger sharks are present to aid escape	3	Change of habitat
Wirsing et al., 2007a	Tiger shark	Dugong	Sea grass	Dugongs alter their foraging tactic according to the level of predation risk	3	Change of behaviour

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